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The den system of the Alpine marmot
(Marmota marmota marmota) in the
National Park of Stelvio, Northern Italy

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Abstract

Studied the den system of the Alpine marmot which consisted of a variable number of chambers, the principal one being lined with thick litter, with openings and tunnels that linked them with the outer surroundings.

Openings were divided into four types which differed in their use and location within the animal's home range.

A qualitative and quantitative analysis of the den system showed a positive correlation between the slope and the opening's orientation; the gradient of the first 30 cm of the tunnel differed between the principal and secondary openings.

Exposure to wind was suggested as the main factor affecting the non-random arrangement of the openings.

Introduction

The behavioural and ecological characteristics in the genus *Marmota* have been studied in detail by ARMITAGE (1962, 1965, 1973, 1974, 1975, 1977, 1979), DOWNHOWER and ARMITAGE (1971), BARASH (1973a, 1973b, 1974a), SVENDSEN (1974). The American researchers by analysing their six Nearctic species obtained a clear picture of the relationships between environment and social structure, and outlined a hypothesis on the evolution of society in the genus *Marmota* (BARASH 1974b) later criticized by ANDERSEN et al. (1976).

In this connection, however, it is surprising the meagre attention paid to some interesting papers on the ecology and psychology of the Alpine marmot previously published (BOPP 1954, 1955, 1956, 1966; MÜLLER-USING 1954, 1956, 1957; PSENNER 1956, 1957, 1960; MÜNCH 1958; COUTURIER 1964; ZELENKA 1965). According to ARMITAGE and DOWNHOWER (1974) the quality of hibernacula (places in which marmots spend the winter) and the quantity of fat accumulated before winter may influence the survival of the young yellow-bellied marmots *(Marmota flaviventris)* through hibernation.

ANDERSEN et al. (1976) suggested that the availability of hibernacula (which were also used during summer) may influence the female reproductive success of yellow-bellied marmot *(M. flaviventris),* and determine the degree of sociality of a species.

KING (1955), in a closely related species, *Cynomys ludovicianus,* pointed out the importance of the relation between the individuals and the den system in determining distinct spatial patterns of their social organization. Moreover, by analysing the characteristics of the black-tailed prairie dog's den system, which lasts from generation to generation, he suggested its stabilizing effect on the organization of the colony.

Therefore, a knowledge of the characteristics of the den system as well as the strategies in the choice of areas to be colonized may be important in the study of social organization and in understanding the adaptation of this rodent to the alpine habitat. The aim of this study is the analysis of the den system of the Alpine marmot.

Description of the den system

According to SCHOCHER (1946 cited in KRAPP 1978) the den system of the Alpine marmot at least consisted of an underground extent (real den) and one ore more openings.

ARMITAGE (1962) considered two types of den in the yellow-bellied marmot *(M. flaviventris):* the home-burrow and the auxiliary burrows. The former were the places where an individual normally spent the night and the young lived; the latter served as place of refuge when an individual was not able to return to the home-burrow.

Similarly, ZELENKA (1965) maintained the existence of a principal den ("terrier principal"), where individuals hibernated and females gave birth, and secondary dens ("terriers secondaires") which were essentially used when a marmot was not able to return to the principal den.

Finally, MERRIAM (1971) considered the frequency of use of each den by eight radio marked woodchucks *(Marmota monax)* and defined the home-burrow as the den which had the greatest frequency of use.

In the present study the den system consisted of den units and incomplete structures. Den units contained a different number of chambers, tunnels departing from them, and openings which linked with the outer surface; incomplete structures were characterized by the lack of a component, either the tunnel or the chamber.

There were two categories of den unit: the pricipal den unit and the flight den unit. The former, located in the central area of the home range, included the principal chamber supplied with litter where the female usually gave birth and the family spent the winter together; it also had other chambers of minor importance. The latter, on the contrary, was located near the border of the home range and its function was purely defensive. Finally, the incomplete structures might have either a defensive function or be used for faecal deposits (latrines).

The openings, on which this study is concentrated, were subdivided by BOPP (1954, 1955, 1956, 1966) into four classes: principal openings, secondary openings, escape openings and openings for faecal deposits.

To distinguish between openings, BOPP considered the functional aspects and the type of link (direct or indirect) with the principal chamber.

Methods

Study area

The present study, conducted during the summers of 1979 and 1980, analysed den systems in the National Park of Stelvio (Val Cedec, Val Zebrù, Val dei Forni, Val di Rabbi, Giogo dello Stelvio, Val Martello), (CAGNOLARO 1969).

The National Park of Stelvio has substantial crystalline metamorphic outcrops (mica-schists and

quartziferous rocks) with outcrops of dolomite and is rich of drifts and fluvial-glacial deposits on the bottom of the valleys.

Marmots occured at an altitude between 1700 and 3000 m but were most abundant between 2100 and 2500 m, the zone in which den systems were surveyed. Marmots were found in areas of metamorphic substratum as well as those with superficial deposit.

The criterion for the selection of the den system to be studied was that the entire structure was situated in superficial deposits, to allow the collection of data and that it was inhabited by a small number of individuals (maximum eight including young) to allow the individual recognition of animals not previously marked.

Distinction between openings

During the field work the animals were watched from their emergence until the end of the daily activity to collect data on the amount of use of each opening. In this evaluation the young's activity was very important since they confine their movements to the area around the principal chamber during the first period of life (ZELENKA 1965), and their fidelity to this chamber is very high (BARASH 1974a).

In identifying the different function and location of the openings, I could distinguish only the category of openings not linked with the principal chamber (i.e. escape openings and openings for faecal deposits). For the other category of openings, belonging to the principal den unit (i.e. principal and secondary openings), I preferred not to consider the type of link with the principal chamber (direct or indirect) used by BOPP (1954, 1955, 1956, 1966). Instead I used the frequency of use of each opening and have tested (with chi-square) the significance of differences in use and, consequently, assigned the classification to the openings. In the den system number three, for example, there were

Table 1

Frequency of use of openings belonging to the principal den unit

| Den systems | Frequency of use of each opening | | | df | X^2 | p |
	A	B	C			
1	278	244	–	1	2.22	> 0.10
2	302	234	–	1	8.62	< 0.01
3	188	142	123	2	14.80	< 0.001
4	239	181	162	2	16.59	< 0.001
5	213	153	138	2	18.76	< 0.001
6	198	128	103	2	33.93	< 0.001
7	236	141	127	2	41.87	< 0.001
8	262	158	138	2	47.66	< 0.001

df = degrees of freedom

three openings (A, B, C) belonging to the principal den unit. However, according to the frequency of use of each opening, opening A (the most used one, 188 times) was considered principal opening while the remaining openings (B, C, used 142 and 123 times respectively) were considered secondary openings (table 1).

In the den system number one there were two openings belonging to the principal den unit. However, according to the frequency of use of each opening, opening A (used 278 times) and opening B (used 244 times) were both considered principal openings since their difference in use was not statistically different (p > 0.10).

The characteristics of the openings

The following characteristics were considered for each opening (fig. 1):
– width: maximum distance between two points linked by an imaginary horizontal line
– height: maximum distance between two points linked by an imaginary vertical line
– area: value given by the multiplication of width by height
– gradient: angle between the imaginary vertical line and the direction of the first 30 cm of the tunnel. This datum was collected by using a self made instrument which consisted of two compass legs, a spirit level attached to the vertical leg and a protractor.
BOPP (1954, 1955, 1956, 1966) used the horizontal line as a reference point from which to collect this
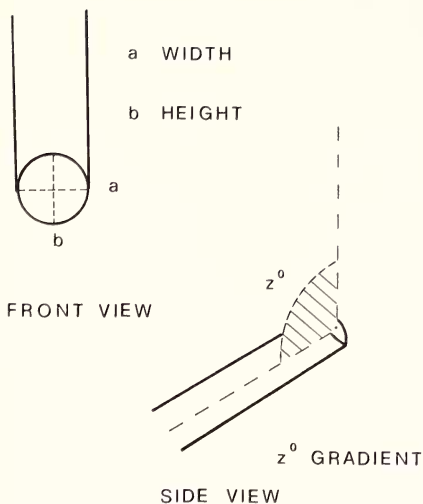
a WIDTH

b HEIGHT

a

b

FRONT VIEW

z^0

z^0 GRADIENT

SIDE VIEW

Fig. 1. Characteristics of the opening

datum but fewer problems were found, working in respect of the vertical line, to reach the exact position for reading the gradient.

– orientation: the direction the opening was facing. To calculate this datum the 360° of the compass were divided into 45° sectors and each value was assigned to the nearest 45° sector.

– quantity of rubble: stones and ground soil found in front of the opening. This characteristic has not been considered in the result section because it was determined subjectively.

Results

Proportion of different types of opening

The most common openings were escape openings (55 %), with fewer secondary openings (22 %) (table 2). Bopp (1954, 1955, 1956, 1966), analysing den systems belonging to families that had colonized either metamorphic substrata or superficial deposits, found 56 % of secondary openings and 13 % of escape openings (N = 104), a proportion which is statistically different from mine (X^2 = 30, df = 1, p < 0.001). The higher proportion of escape openings found in my sample is probably due to the distance between the site in which the principal den unit was located and the feeding areas ($\bar{x}$ = 90 m, S.D. = ± 33 m). The value of such distance was determined every 15 minutes by considering the space between the principal opening and the point in which the marmots were feeding.

Table 2

Distribution of the openings between the four classes

Den systems	P. O.	S. O.	E. O.	F. O.	N
8	9	13	33	5	60

P. O. = Principal openings; S. O. = Secondary openings; E. O. = Escape openings; F. O. = Openings for faecal deposits; N = total openings.

The shape of the opening

From table 3, the shape of the opening was circular and the standard error of width and height were similar. However, according to Lattmann (1973 cited in Krapp 1978) the openings have the width which is frequently bigger than the height.

Bopp (1956, 1966), in a smaller sample (N = 46), obtained values that did not differ significantly from mine (Mann-Whitney U test) for width (U = 1346, z = − 0.22, p > 0.80), height (U = 1446, z = 0.42, p > 0.60) and area (U = 1300, z = −0.51, p > 0.60).

The individual characteristics of the openings may also be considered in relation to the various classes of opening to which they belong (table 3).

Table 3

Mean value and standard error (±) of individual characteristics for each class of opening and total openings (N)

Characteristic	P. O.	S. O.	E. O.	F. O.	N
Width (cm)	28 ± 7	25 ± 2	21 ± 1	23 ± 3	23 ± 1
Height (cm)	25 ± 3	26 ± 2	21 ± 1	23 ± 7	23 ± 1
Area (cm²)	737 ± 227	701 ± 118	446 ± 27	556 ± 238	555 ± 50
Gradient	125° ± 4°	112° ± 4°	115° ± 2°	107° ± 3°	115° ± 2°

Statistical analysis (Mann-Whitney U test)

Height:	S. O.	v	E. O.	$U = 136$	$z = -1.93$	$p < 0.05$
Area:	S. O.	v	E. O.	$U = 126$	$z = -2.16$	$p < 0.05$
Gradient:	P. O.	v	S. O.	$U = 32.5$	$n_1 = 9; n_2 = 13$	$p < 0.05$
	P. O.	v	E. O.	$U = 88$	$z = -1.86$	$p < 0.05$
	P. O.	v	F. O.	$U = 1$	$n_1 = 5; n_2 = 9$	$p < 0.001$
	E. O.	v	F. O.	$U = 42$	$z = -1.75$	$p < 0.05$

v   versus

Width

The principal opening was bigger than the secondary opening but there were no statistical differences between classes of opening. The principal opening showed a large standard error value.

Height

This was similar in the principal opening and secondary opening as well as in escape opening and opening for faecal deposits. However, secondary openings were significantly bigger than escape openings ($p < 0.05$). The class of opening for faecal deposits showed a large standard error value.

Area

This was bigger in the principal opening than in the secondary opening. BARASH (1976) also found that the principal opening (defining this as the entrance used to reach the chamber in which animals hibernate) had a cross sectional area bigger than that of other openings ($p < 0.05$).

However, using his system applied to the different classes of opening in the present study, the difference between principal and secondary opening was not significant ($p > 0.10$). In the present study, secondary openings were significantly bigger than escape openings ($p < 0.05$). The class of principal opening and opening for faecal deposits showed a large standard error value.

Gradient

The principal opening had a steeper gradient than the secondary opening, and, interestingly, the mean gradient of escape openings was equal to that of total openings ($N = 60$). The principal openings were significantly steeper than all the other classes of opening (at the 0.05 level or more); moreover escape openings were significantly steeper than openings for faecal deposits ($p < 0.05$).

The standard error value was very small in each class of opening.

Bopp (1956, 1966) found a gradient that (after relating his data to the vertical line) was significantly steeper than the data of the present study (U = 669, z = − 4.54, p < 0.001).

Orientation

The distribution of the values between the possible directions is shown in fig. 3(a): only six openings (10 %) faced North of the East-West line while 39 openings (65 %) faced South. The analysis of such circular data (BATSCHELET 1965) gave a value of r (polar coordinate of the mean vector) of 0.43 and a mean orientation angle theta (polar coordinate of the mean vector) of 276°. The mean angular deviation s was 61° (fig. 2).
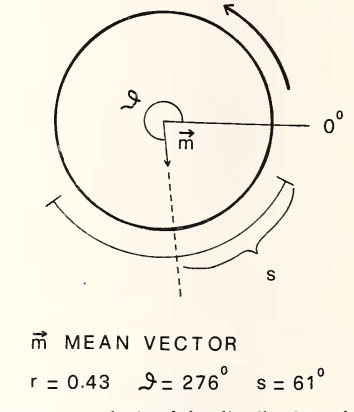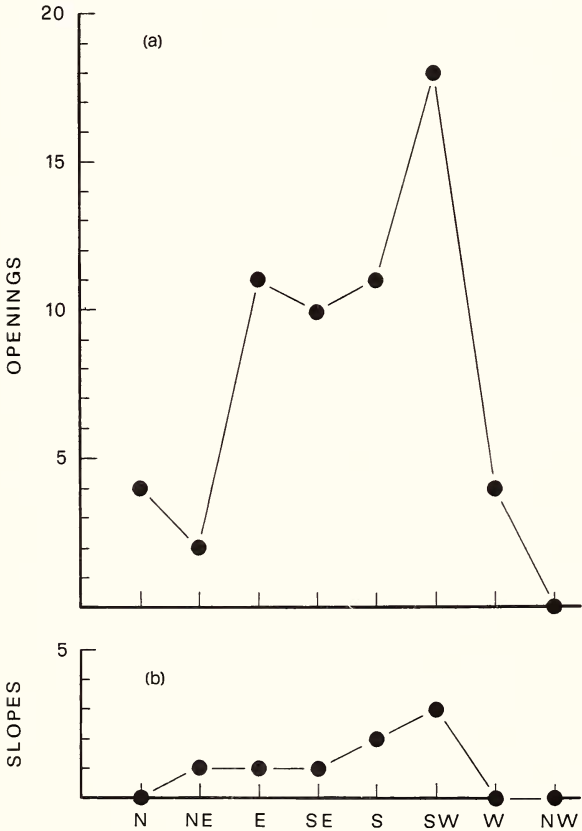

$\vec{m}$ MEAN VECTOR

r = 0.43 ϑ = 276°   s = 61°

Fig. 2. Analysis of the distribution of the opening orientation

Fig. 3. Orientation of the openings (a) and the slopes (b)

A statistical test of randomness (Rayleigh test; BATSCHELET 1965) suggested the rejection of the null hypothesis of a uniform distribution (z = 10.9, p < 0.001).

There was a significant correlation between the orientation of the slope (fig. 3) and of the opening (Spearman rank correlation coefficient r_s = 0.79, p < 0.05; SIEGEL 1956).

Interestingly, Bopp (1954, 1955, 1956) found 12 % of the openings facing North of the East-West line and 66 % of the openings facing South, a proportion similar to that of the present study.

According to COUTURIER (1964) the openings were rarely oriented northwards and their orientation was highly variable. However, the analysis of a colonial territory (BOPP 1966) facing NNE showed a clear orientation of the openings northwards (84 % of the

openings North of the East-West line and 0 % of the openings South), thus suggesting the possible existence of the correlation between slope and opening orientation before mentioned.

Finally, BARASH (1973a) found only two colony slopes of *Marmota olympus* (10.5 %) facing North of the East-West line and 15 colony slopes (79 %) facing South; these data did not significantly differ from those of the present study (Fisher exact probability test, $p > 0.60$).

Discussion

The gradient is the only characteristic of the opening which has a different distribution of values between the principal and secondary class of opening. All the other characteristics have values which differ between openings belonging to the principal den unit and openings not linked with the principal chamber (or between the latter).

However, the problem of finding a discriminant characteristic between the principal and secondary opening is still unsolved.

The next step could be the evaluation of data on the characteristics of the opening by means of a multivariate analysis, using discriminant functions applied to a larger sample of openings (SOKAL and ROHLF 1969).

Many physical and biological factors may affect the opening characteristics: the composition of the soil, the inclination of the slope, the predatory pressure, the number of individuals in the social group, etc. Wind, in particular, may affect the orientation and location of the openings determining areas to be colonized. In fact, the greatest divergence in the orientation of the openings was probably related to the direction of winds; the only openings oriented North were found where winds blew from the South.

This possible correlation is supported by the observation of the activity of animals, belonging to den systems differently oriented to the wind, in adverse weather conditions. In June marmots were usually active during wind storms except for the individuals which had colonized slopes oriented in a direction facing the wind storm.

According to SVENDSEN (1974) yellow-bellied marmots *(M. flavivientris)* spent 80 % of their lives underground and almost 60 % in hibernation. Den site selection may therefore be critical. It may be linked with the degree of protection provided by the snow cover (SVENDSEN 1974; MÜLLER-USING 1956; ZELENKA 1965) and the temperature variations that occur in spring during the snow melting when the exausted animals have just roused from hibernation.

At this time the animal is particularly sensitive to sudden variations (again, possible wind action) and its survival may depend on their prevention. The orientation of the opening and the gradient of the tunnel (in relation to the vertical line) may play an important role in reducing the effect of the wind at this vulnerable time.

However, more detailed research on the den system is necessary to understand its importance and influence on the behavioural ecology of the marmot.

Zusammenfassung

Das Gangsystem des Alpenmurmeltieres (Marmota marmota marmota) im Nationalpark Stelvio, Nord-Italien

Untersucht wurden Baue von Alpenmurmeltieren. Man kann Hauptbaue, die die Nestkammer und mehrere Zugänge enthalten, und Nebenbaue unterscheiden, die als Fluchtröhren oder Latrinen dienen. Die am häufigsten benutzten Zugänge zum Hauptbau wurden als Hauptzugänge, die anderen als Nebenzugänge bezeichnet. Größe, Neigung und Orientierung der verschiedenen Kategorien von Zugängen werden verglichen. Besonders in der Steilheit bestehen Unterschiede. Die Zugänge öffnen sich überwiegend nach Süden, dort wird ihre Orientierung vermutlich entscheidend durch die Hauptwindrichtung beeinflußt.

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Zur Fortpflanzungsbiologie des Zebraduckers *Cephalophus zebra* (Gray, 1838) im Vergleich zu anderen *Cephalophus*-Arten[1]

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Eingang des Ms. 18. 5. 1983

Abstract

On the reproductive biology of the Banded duiker Cephalophus zebra (Gray, 1838) in comparison with other species of Cephalophus

The reproductive biology of the Banded duiker was studied over a period of ten months as part of a "Staatsexamensarbeit". This was compared with the known habits of other *Cephalophus* species. Fertility was observed to return ten days after birth. The courting behavior as well as the changes in the female during the gestation period were described. The gestation period was determined to be 221 to 229 days for *C. zebra*.

Furthermore, the birth of two *C. zebra* was observed and compared with those of other species. The behavior patterns between parents and offspring were studied in detail as was the development of the young. This included weight development, body maturation, sexual development, maturing behavior patterns, development phases in nutrition, mobility, curiosity and play behavior.

Einleitung

Über die Fortpflanzungsbiologie der Duckerantilopen (Cephalophinae; Bovidae) ist relativ wenig bekannt. Epigame Verhaltensweisen sowie die Fortpflanzung selbst scheinen nicht jahreszeitlich gebunden zu sein (Dittrich 1972a; Haltenorth und Diller 1977; von Ketelhodt 1977a); der Erfolg einer Paarung ist daher ausschließlich von den Östrusperioden der ♀♀ abhängig.

Nahezu nichts war bisher über die Fortpflanzung des seltenen Zebraduckers *Cephalophus zebra* (Gray, 1838) bekannt, dessen Verbreitungsgebiet auf die Regenwaldzonen

[1] Nach einem Vortrag, gehalten anläßlich der 53. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 27. 9. 1979 in Zürich.